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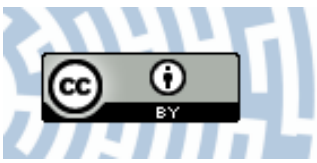

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RESEARCH PAPER

# Role of spatial and environmental factors in shaping the rotifer metacommunity in anthropogenic water bodies

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**Abstract** In spatially heterogeneous habitats, local communities may be shaped by both local biotic and abiotic factors and by regional factors (dispersal of individuals among habitats). In recent years, ecologists have been increasingly interested in measuring how much the structure of local communities is explained by spatial variables and by non-spatial environmental variables. We analysed the effects of biotic and abiotic factors on rotifer communities in 12 anthropogenic water bodies in the Silesian Upland. The studies were conducted in two groups of water bodies which were of differing dimensions: group A — seven water bodies situated very close to each other (between 50 and 500 m), group B — the water bodies from group A as well as 5 other water bodies situated 2 km away, which were at greater distances from each other (about 1–3 km). Apart from this, genetic variation was assessed in 3 populations of *Brachionus plicatilis* Müller to estimate the level of gene flow between them. A characteristic feature of anthropogenic water bodies is a high variation in environmental conditions, so they are specific and difficult habitats for many organisms. Our study shows that environmental factors played a major role in shaping the local rotifer communities in heterogeneous anthropogenic water bodies with respect to salinity. Results of this study suggest, however, that in neighbouring water bodies, dispersal is very important for maintenance of local species diversity. A medium level of genetic variation between populations of *B. plicatilis* indicates that gene flow occurs irrespective of the distance between local populations.

**Keywords** Environmental conditions · Dispersal · Heterogeneous water bodies · *Brachionus plicatilis* · Genetic variation

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## Introduction

When assessing the biodiversity of habitats varying in spatial and non-spatial environmental conditions, it is important to analyse local communities at a broader, regional scale. This applies mostly to populations living in habitats composed of more or less isolated patches. Local populations inhabiting such discrete patches may be subject to random dispersal and extinction (Hanski and Gilpin 1991; Bengtsson and Ebert 1998).

The idea that colonization and extinction may determine the structure of local communities through dispersal was first described in ecology by the island biogeography theory (MacArthur and Wilson 1967). This theory attempted to predict the number of species that would exist on a newly created island. It also explained how distance and area combine to regulate the balance between immigration and extinction in an island population.

It assumes that fragmented habitats (small areas of the habitat) are colonized from a large, major habitat. In the 1970s, Richard Levins coined the term *metapopulation*, which denotes a group of local populations of a species,

which are linked with one another through dispersal (Hanski and Gilpin 1991). However, in the metapopulation model, there is no main source of colonists. The concept of metapopulation has formed a basis for the concept of metacommunity. It denotes a group of local communities which are linked through dispersal of the numerous interacting species (Hanski and Gilpin 1991; Wilson 1992; Hubbell 2001; Leibold and Mikkelson 2002).

The concepts of metapopulation and metacommunity are extremely important for the assessment of factors that determine the distribution of organisms in spatially heterogeneous habitats, where there are unequally distributed environmental characteristics (temperature, salinity etc.). Local communities may be shaped simultaneously by both local factors (habitat conditions, competition, predation) and regional factors (dispersal of individuals among habitats) (Pinel-Alloul et al. 1995; Cottenie et al. 2003; Havel and Shurin 2004). Considering that biotic and abiotic factors vary in space, an important goal of ecology is to assess the effects of spatial factors on populations and communities (Magnan et al. 1994). Thanks to investigations into how much of the variation in metacommunity structure is explained by non-spatial environmental factors and by spatial factors (dispersal) e.g. Borcard et al. 1992), 4 paradigms of metacommunities were distinguished by Leibold et al. (2004): (1) the patch-dynamic view (PD), which assumes habitat homogeneity, where local species diversity is limited by dispersal; (2) the species-sorting view (SS), which assumes that the habitat is heterogeneous, and both patch quality and moderate dispersal affect the local diversity of communities; (3) the mass-effect view (ME), which emphasizes the role of high dispersal and spatial dynamics, resulting from the source-sink effect in the heterogeneous habitat; and (4) the neutral model view (NM), where all species are similarly competitive, mobile or adaptable, and community structure is shaped by random dispersal.

In recent years, ecologists have focused on the development of a method that would enable practical application of the 4 theoretical paradigms listed above. On the basis of meta-analyses of a large group of communities, Cottenie (2005) developed a decision tree which combines theoretical models of metacommunities (Leibold et al. 2004) with empirical data.

Rotifer species inhabiting inland water bodies are a perfect model for studies of metacommunities because water bodies — like islands — have well-defined boundaries (Cottenie et al. 2003). Moreover, rotifers can be passively transported between water bodies by wind, rain or animals (Havel et al. 2002; Havel and Shurin 2004).

Valuable data on the effects of dispersal and environmental conditions on local rotifer communities can be supplied by the use of molecular tools. Microsatellites are used by molecular ecologists to answer questions concerning population structure, migration and gene flow, reproduction patterns, origin, and identification of individuals and clones (Jarne and Lagoda 1996; Feral 2002; Gómez et al. 2002b; Chistiakov et al. 2006; Evanno et al. 2009; Papakostas et al. 2009). In rotifers, microsatellite markers have been identified so far only for *Brachionus plicatilis* s.s. Müller. The network of 7 microsatellite loci (*Bp1b, Bp2, Bp3, Bp3c, Bp4a, Bp5d, Bp6b*) described by Gómez et al. (1998) for *B. plicatilis* s.s. is a very informative tool for research on population structure. Molecular research on *B. plicatilis* individuals collected in field conditions can help to explain how the metapopulation is formed, not only for this species but also for other planktonic rotifers.

An analysis of rotifer communities in anthropogenic water bodies at a local and regional scale can provide valuable information on their ability to adapt to local environmental conditions, and their potential for colonizing new habitats. Biodiversity research at a regional scale is extremely important in anthropogenic water bodies because their creation results in the formation of new habitats that can be colonized. They may also be temporary sites for many organisms.

We test two hypotheses in this study:

1. Environmental factors in anthropogenic water bodies affect the structure of local rotifer communities more strongly than do spatial factors.
2. In habitats where environmental conditions are highly variable, dispersal plays a more important role than in more stable habitats.

In relation to these hypotheses, we performed the following tests: (a) assessment of the role of environmental and spatial conditions in shaping the rotifer metacommunity in 12 isolated anthropogenic water bodies at 2 spatial scales; (b) determination of the model of the rotifer metacommunity; and (c) assessment of the level of gene flow between 3 populations of *B. plicatilis*, through an analysis of intra- and interpopulation genetic variation.

## Materials and methods

### Study area

We collected the material for this study from 12 isolated, highly heterogeneous, anthropogenic water bodies that differ significantly in the physicochemical properties of the waters (Table 1). The water bodies are located in the town of Knurów in the Silesian Upland (southern Poland). They include 8 mining subsidence pools, 2 flood ponds, and 2 flooded borrow pits. The anthropogenic water bodies are

**Table 1** Characteristics of investigated water bodies (average values ± SD) in April–November 2008–2010

| Factor | A1 | A2G | A3 | A4 | A5 | A6 | A7G | B8 | B9 | B10G | B11 | B12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Temperature (°C) | 17.90 ± 5.77 | 18.67 ± 6.17 | 18.43 ± 5.65 | 17.53 ± 5.61 | 18.61 ± 5.39 | 18.10 ± 6.01 | 19.20 ± 5.81 | 18.60 ± 5.64 | 22.50 ± 4.82 | 17.87 ± 5.19 | 17.20 ± 5.39 | 17.47 ± 5.61 |
| pH | 8.46 ± 0.59 | 8.24 ± 0.53 | 7.91 ± 0.50 | 7.85 ± 0.33 | 7.96 ± 0.30 | 8.29 ± 0.27 | 7.89 ± 0.30 | 7.02 ± 0.46 | 7.23 ± 0.11 | 8.25 ± 0.28 | 7.95 ± 0.49 | 7.81 ± 0.28 |
| Dissolved $O_2$ (mg $dm^{-3}$) | 9.95 ± 1.76 | 13.12 ± 2.66 | 9.91 ± 1.60 | 8.27 ± 1.48 | 8.80 ± 1.55 | 9.83 ± 2.83 | 11.15 ± 3.76 | 8.85 ± 1.50 | 7.57 ± 2.49 | 9.49 ± 1.73 | 10.84 ± 1.72 | 8.79 ± 1.84 |
| TDS (mg $dm^{-3}$) | 216.00 ± 18.05 | 2,616.00 ± 1,368.08 | 1,090.67 ± 246.59 | 1,115.33 ± 77.91 | 1,756.43 ± 190.13 | 3,375.00 ± 372.52 | 5,314.67 ± 830.46 | 157.33 ± 13.87 | 29,390.00 ± 3,670.04 | 3,696.00 ± 213.90 | 334.67 ± 25.32 | 1,705.33 ± 236.40 |
| $NO_3$ (mg $dm^{-3}$) | 2.03 ± 1.74 | 0.75 ± 1.67 | 0.41 ± 0.69 | 0.31 ± 0.63 | 0.27 ± 0.42 | 0.59 ± 0.89 | 0.30 ± 0.64 | 0.93 ± 1.07 | 3.83 ± 1.61 | 0.69 ± 0.85 | 0.42 ± 0.60 | 0.59 ± 0.84 |
| $PO_4$ (mg $dm^{-3}$) | 0.42± 0.51 | 0.46 ± 0.26 | 0.74 ± 0.57 | 0.62 ± 0.60 | 0.59 ± 0.49 | 0.52 ± 0.60 | 0.76 ± 0.69 | 0.51 ± 0.45 | 0.72 ± 0.72 | 0.73 ± 0.79 | 0.60 ± 0.46 | 0.58 ± 0.41 |
| Bottom type | gravel-silty | silty | gravel | gravel | gravel-silty | gravel-silty | silty | silty-sandy | gravel-silty | silty | sandy-silty | gravel-silty |
| Origin | subsidence | subsidence | subsidence | subsidence | after flooding | after flooding | subsidence | subsidence | borrow pit | borrow pit | subsidence | subsidence |
| Year of creation | 1971 | 1964 | 1971 | 1971 | 1997 | 1997 | 1973 | 1974 | 1974 | 1974 | 1974 | 1977 |

*TDS* total dissolved solids

characterized by high dynamics and relatively small size (ranging from 0.21 to 16 ha in area, generally shallow). The water bodies included in the study are situated in an area of hard bituminous coal mining. Mining activity influences the salinity of the waters. The water bodies were divided into 4 groups in respect of water salinity on the basis of mean concentration of total dissolved solids (TDS) (Table 1): freshwater ponds, TDS <500 mg $dm^{-3}$; subsaline ponds, TDS = 500–3,000 mg $dm^{-3}$; hyposaline ponds, TDS = 3,000–20,000 mg $dm^{-3}$; and mesosaline ponds, TDS = 20,000–50,000 mg $dm^{-3}$, based on Hammer (1986).

We assessed the geographic coordinates of the water bodies using a GPS receiver.

We conducted the research in 2 groups representing different spatial scales: group A = 7 water bodies located very close to one another (50–400 m apart); group B = water bodies of group A and 5 water bodies located more than 2 km away from them and more distant from one another (about 1–3 km, Fig. 1).

Distances between the 3 water bodies where samples were collected for genetic analysis of *B. plicatilis* varied from 1 to 3.5 km. Two of them were located within group A and the third one was outside that group.

## Sampling procedure

We collected the material for this study every 2 weeks in 2008–2010. Each time we collected 5 quantitative samples (and treated them as replications) from the littoral zone of each water body. Each sample was obtained by filtering 10 $dm^3$ of water through a plankton sieve (mesh size 25 μm), next the sample volume was reduced to 0.05 $dm^3$, and preserved with a mixture of formalin, glycerol, and water (3:1:6). Individuals of each rotifer species were counted in Kolkwitz chambers (0.001 $dm^3$). We calculated a mean abundance for 5 chambers and expressed this per $dm^3$.

From 3 water bodies (A2G, A7G, and B10G), we took additional samples for assessment of microsatellite DNA polymorphism in live specimens of *B. plicatilis*. These water bodies were selected for genetic analyses because their *B. plicatilis* populations were most stable. The DNA analyses were based on 30 individuals from population A2G, 34 individuals from A7G, and 33 individuals from B10G. The analyses followed the protocol of Gómez et al. (1998). Microsatellite genotyping PCR conditions used in this study were: 7.5 pM primers labelled with TAM, FAM, HEX, 0.25 mM of each dNTP, 2 mM $MgCl_2$ and 0.6 U of Taq polymerase (Invitrogen, Life Technologies) in PCR buffer with genomic DNA. All primer sequences and names were from Gómez et al. (1998). Microsatellites were amplified using a Biometra TProfessional thermal cycler for 10 min at 95 °C, followed by 30–35 cycles of 30 s at 95 °C, 30 s at 58 °C and 45 s at 72 °C and 10 min at 72 °C.

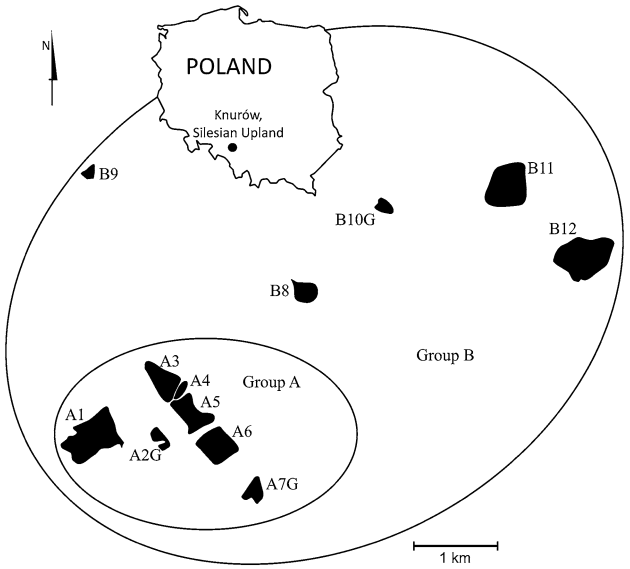


**Fig. 1** Location of study area. The letters correspond to the designated groups, depending on the distance of the reservoirs. The letter G shows reservoirs from which individuals of *B. plicatilis* were obtained for genetic testing

Positive PCR products were separated on the ABI PRISM 3100 Genetic Analyser using GeneScan 2.0 (Perkin-Elmer Applied Biosystems), using standard laboratory conditions as described by the manufacturers (Wenz et al. 1998). A mixture containing HiDiFormamide, the PCR product and a size standard (alleles were sized against an internal size standard, RoxGS500), was denatured and loaded onto a POP4 acrylamide gel and subsequently automatically analysed on a PeakScanner1.0 (Applied Biosystems).

When collecting the water samples for biological research, we took a separate sample for analysis of selected physicochemical properties: temperature, pH, dissolved oxygen, TDS, nitrates, and phosphates. The physicochemical parameters were analysed using Merck kits for assessment of oxygen content and chloride concentration; and a Hanna portable meter (HI 9811-5) for measurements of pH, conductivity, and TDS, nitrates, and phosphates.

## Statistical analysis

We investigated the simultaneous effects of environmental and spatial variables by means of canonical correspondence analysis (CCA) and partial CCA. Before analysis, the data were subjected to log transformation and centering. Spatial variables based on coordinates $x$ and $y$ were complemented as suggested by Legendre (1990) with cubic trend surface regression, according to the equation:

$$\hat{z} = b_1 x + b_2 y + b_3 x^2 + b_4 xy + b_5 y^2 + b_6 x^3 + b_7 x^2 y + b_8 xy^2 + b_9 y^3$$

During CCA, we used forward selection to identify the variables that affected the rotifer communities most strongly (the analyses included only variables significant at $P < 0.1$, verified on the basis of a Monte Carlo permutation test for 499 replications). Using the methods proposed by Borcard et al. (1992) and Cottenie (2005), we separated the variation observed in the rotifer communities into independent fractions explained by environmental or spatial variables: [$E$], environmental variation; [$S$], spatial variation; [$E|S$], environmental variation after removing the effect of spatial components (pure environmental); [$S|E$], spatial variation after removing the effect of environmental components (pure spatial); [$E + S$], total explained variation; $1 - [E + S]$, unexplained variation; and [$E$ with $S$], variation from correlations between environmental and spatial variables. Statistical significance of CCA and partial CCA was verified by a Monte Carlo permutation test for 499 replications. Ordination analyses were performed by CANOCO 4.5 for Windows software (Ter Braak and Šmilauer 2002). On the basis of their significance, we classified the rotifer metacommunity as one of the models (SS, ME, NM, PD) by using the decision tree proposed by Cottenie (2005). If only environmental variables are significant, the metacommunity corresponds to the SS model. If both environmental and spatial variables are significant, then the SS model is combined with ME (basically, the SS model with a stronger effect of dispersal on the structure of local communities than in the perfect SS model). If only spatial variables are significant, then the metacommunity structure is shaped mostly by strong dispersal (either the NM or PD model).

To assess the degree of polymorphism of microsatellite loci (*Bp1b*, *Bp2*, *Bp3*, *Bp3c*, *Bp4a*, *Bp5d*, and *Bp6b*) in populations of *B. plicatilis*, we estimated the allele number in each locus for the given population ($A_N$), allele frequencies in individual loci, number of alleles characteristic for individual populations, expected heterozygosity ($H_e$), and observed heterozygosity ($H_o$), by using GENETIX 4.05.2 software (Belkhir et al. 1996). Probability of deviations from Hardy–Weinberg equilibrium for each population was assessed by using the exact test (Guo and Thompson 1992) implemented in GENEPOP 3.4 software (Raymond and Rousset 1995). Statistical significance of deviations from the equilibrium was assessed by using the Bonferroni sequential correction (Rice 1989).

To determine the degree of inbreeding, i.e. the ratio of observed heterozygosity to expected heterozygosity within the population and randomness of mating, we calculated the inbreeding coefficient $F_{IS}$. Fstat 2.9.3.2. software (Goudet 1995, 2001) was used to estimate the fixation index $F_{ST}$, which is a measure of population differentiation ($\theta$-statistics, Weir and Cockerham 1984; Goudet et al. 1996).

## Results

### Group A: water bodies located 50–400 m apart

After step-wise selection of environmental and spatial data, only 2 environmental variables (TDS and nitrates) and 3 spatial variables ($x$, $y$, and $x^2$) were included in CCA and partial CCA in group A.

Figure 2 shows the relative significance of the processes that control the variation in rotifer communities at 2 spatial scales: the pure environmental fraction [$E|S$], the spatially structured environmental fraction [$E$ with $S$], the pure spatial fraction [$S|E$] and the undetermined fraction 1 − [$E$ with $S$].

The environmental variables (TDS and nitrates) and spatial ones explain jointly over 93 % of the variation in rotifer communities in the group of anthropogenic water bodies located close to one another (A). The contribution of environmental variables [$E$] was high (64 %) and significant ($P = 0.012$, Table 2). The effect of spatial variables [$S$] was even higher (78.2 %) and also significant ($P = 0.006$). However, the pure environmental effect [$E|S$] and pure spatial effect [$S|E$] were much lower (14.6 and 29.4 %, respectively) and non-significant ($P = 0.392$ and $P = 0.384$, respectively, Table 2). A comparison of fraction [$E|S$] to [$E$] (14.6/64 = 23 %) indicates that the effect of environmental variables on rotifer communities is strongly dependent on the geographic location of water bodies.

The high value of [$E$ with $S$] (49.3 %) and the lack of significance of pure spatial variables indicate that most of the spatial variation in rotifer communities (78.2 %) between neighbouring anthropogenic water bodies is explained by the spatial distribution of environmental factors (Figs. 2, 3). This is evident by the overlapping fragments of environmental and spatial variability shown in Fig. 3.

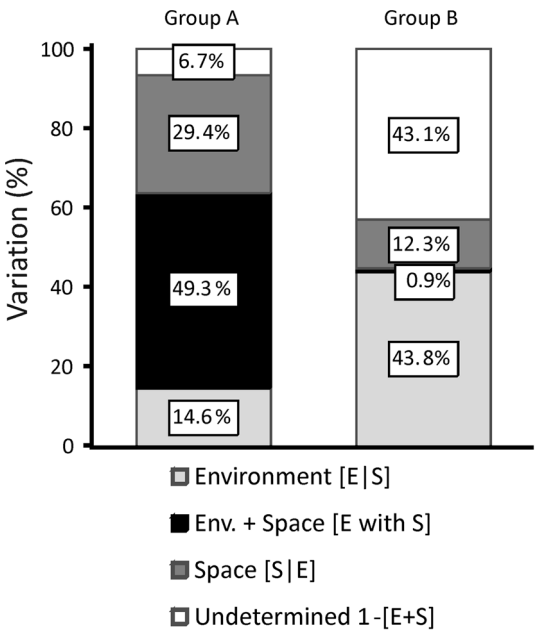


**Fig. 2** Variation partitioning of the Rotifera data matrix according to different spatial scales (group A and group B)

**Table 2** $P$ values of the explanatory components in structuring rotifer communities at spatial scales A and B

| Group | [$E$] | [$S$] | [$E|S$] | [$S|E$] |
|---|---|---|---|---|
| A | 0.012 | 0.006 | 0.392 | 0.384 |
| B | 0.010 | 0.828 | 0.026 | 0.589 |

*[E]* environmental effects, *[S]* spatial effects, *[E|S]* pure environmental effects, *[S|E]* pure spatial effects

In this group of water bodies, we failed to determine unambiguously the metacommunity model with the use of the decision tree, but it seems that environmental conditions and dispersal are equally important. The model represented by the rotifer metacommunity in water bodies of group A is close to the SS + ME model.

### Group B: water bodies located up to about 3.5 km apart

The step-wise selection of environmental and spatial data in group B of water bodies allowed the inclusion in CCA and partial CCA of 3 environmental variables (phosphates, pH, and oxygen) and 2 spatial variables ($x^2$, and $y$).

In group B, involving a larger spatial scale, environmental and spatial variation explained 56.9 % of the variation in rotifer communities, i.e. much less than in group A. The contribution of environmental variables [$E$] to explaining the variation of rotifers was high (44.7 %) and significant ($P = 0.01$, Table 2). Pure environmental effect [$E|S$] was also high (43.8 %) and significant ($P = 0.026$). In contrast, contributions of spatial variables (both [$S$] and [$S|E$]) were low (13.2 and 12.3 %, respectively) and non-significant ($P = 0.828$ and $P = 0.589$, respectively).

The low value of [$E$ with $S$] (0.9 %) indicates that the spatial variation of rotifer communities at a larger spatial scale is only slightly dependent on the spatial distribution of environmental factors. This is to be seen clearly in Fig. 3 where only small fragments of environmental and spatial variability blocks overlap. A comparison of fraction [$E|S$] to [$E$] (43.8/44.7 = 98 %) indicates that the effect of environmental variables on zooplankton is very much the same irrespective of the geographic location of water bodies.

A high proportion of the variation of rotifer communities is still unexplained (43.1 %). This indicates that some other external factors (local biotic and abiotic factors, community dynamics), not taken into account in this study, may affect the structure of local communities.

Statistical significance of the effect of environmental variables (both [$E$] and [$E|S$]) and the lack of significant effect of spatial variables (both [$S$] and [$S|E$]) indicates that

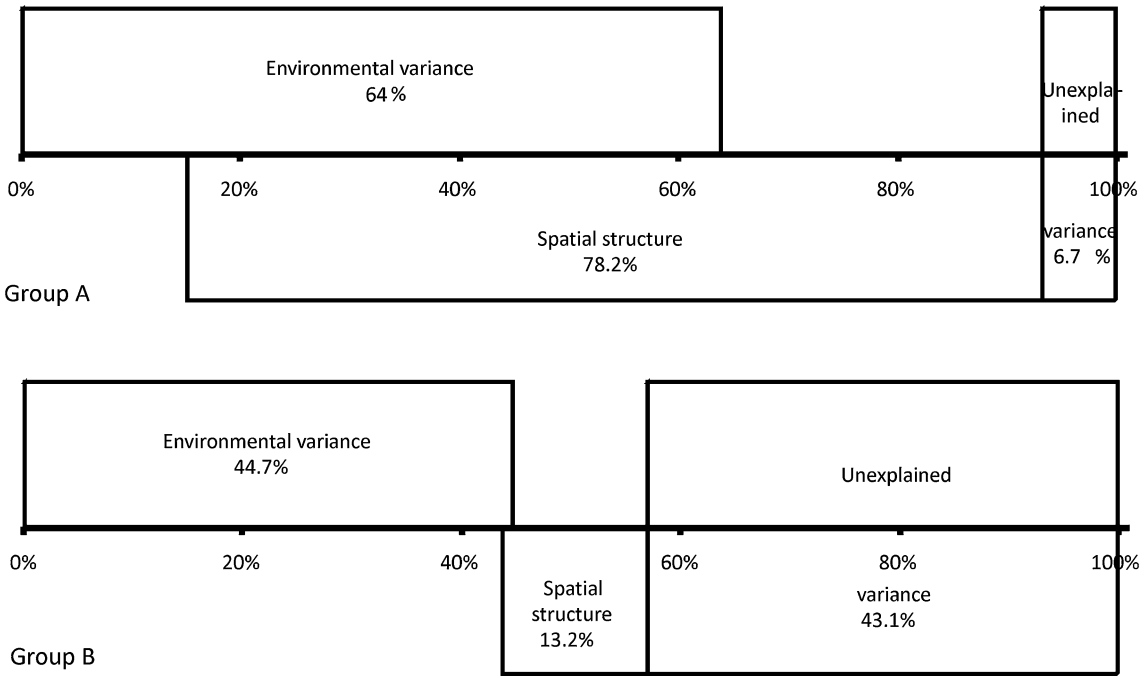


**Fig. 3** Variation partitioning of the Rotifera data matrix, showing comparison size fraction [*E* with *S*], which is an intersection of the environmental and spatial components of the species variation, in groups A and B

the rotifer metacommunity at a larger spatial scale represents the SS model according to the decision tree proposed by Cottenie (2005).

Genetic variation of the metapopulation of *B. plicatilis*

In total, 39 alleles were identified in the analysed samples of *B. plicatilis* (Table 3). The allele number was lowest in population A2G (17), and the highest in population A7G (31). The number of alleles per locus varied from 2 to 5 in population B10G, from 1 to 4 in population A2G, and from 1 to 6 in population A7G (Table 4). Some of the alleles were limited to single samples (Table 3). Generally, loci *Bp2* and *Bp3c* (with 7 alleles) were the most polymorphic. Based on allele frequencies, all 7 loci were classified as polymorphic for population B10G, compared to 6 polymorphic loci for population A7G (*Bp1b*, *Bp2*, *Bp3*, *Bp3c*, *Bp5d*, and *Bp6b*), and 5 polymorphic loci (*Bp1b*, *Bp2*, *Bp3*, *Bp5d*, and *Bp6b*) for population A2G (Table 3). A locus was classified as polymorphic if the frequency of the most common allele was lower than 95 %.

Probabilities of deviations from the Hardy–Weinberg equilibrium suggest that the analysed populations are not balanced genetically (Table 4). Inbreeding coefficients for many loci in all the populations indicate an excess of heterozygotes (Table 4).

The calculated values of $F_{ST}$ indicate a moderate level of differentiation between the studied populations. $F_{ST}$ values varied from 0.0517 (B10G and A7G) to 0.1016 (B10G and A2G). All the values were significant (Table 5). Both the highest and the lowest genetic differentiation were recorded between populations from the most distant water bodies.

## Discussion

The halophilous species in this study, *B. plicatilis*, was observed regularly in hypo- to mesosaline waters (Bielańska-Grajner and Cudak 2014). In earlier studies, *B. plicatilis* was recorded in Upper Silesia in polluted water from mines (Widuto 1984). This species is usually a dominant in various internal saline ecosystems (Arora and Mehra 2009). Timms (2001) observed, in Werewilka Inlet (Lake Wyara) which is highly variable in area and salinity, *B. plicatilis* in the 3.7–55.5 g/dm$^3$ range of salinity.

The structure of local communities of zooplankton can be driven by local environmental factors and regional processes, such as dispersal (Havel and Shurin 2004). Results of our study indicate that the metacommunity structure reflects the SS model in group B, while at a smaller spatial scale (in group A), it is close to the SS + ME model. Leibold et al. (2004) report that plankton in isolated water bodies are a very good example of the SS model. As suggested by Cottenie (2005), most of the communities found in heterogeneous habitats represent this metacommunity type. The SS model was also observed by Pinel-Alloul et al. (1995) in the metacommunity structure

**Table 3** Allele frequencies of 7 microsatellite loci in 3 populations of *B. plicatilis*

| Locus and allele | | Population | | |
|---|---|---|---|---|
| | | A2G $N = 30$ | A7G $N = 34$ | B10G $N = 33$ |
| Bp1b | 230 | – | – | 0.02 |
| | 236 | 0.37 | 0.44 | 0.42 |
| | 239 | – | 0.01 | – |
| | 242 | 0.57 | 0.47 | 0.45 |
| | 245 | 0.07 | 0.07 | 0.02 |
| | 260 | – | – | 0.09 |
| Bp2 | 127 | 0.07 | 0.10 | – |
| | 136 | – | – | 0.02 |
| | 139 | 0.43 | 0.41 | 0.48 |
| | 142 | 0.07 | 0.06 | – |
| | 154 | – | 0.03 | – |
| | 157 | 0.43 | 0.37 | 0.50 |
| | 163 | – | 0.03 | – |
| Bp3 | 150 | – | 0.03 | 0.02 |
| | 153 | 0.50 | 0.29 | 0.42 |
| | 156 | – | 0.19 | – |
| | 159 | – | – | 0.14 |
| | 165 | – | 0.16 | – |
| | 168 | 0.50 | 0.32 | 0.42 |
| Bp3c | 235 | – | 0.03 | – |
| | 238 | 0.03 | – | – |
| | 244 | – | 0.19 | 0.33 |
| | 247 | – | 0.12 | 0.21 |
| | 253 | – | 0.01 | 0.03 |
| | 256 | 0.97 | 0.63 | 0.42 |
| | 277 | – | 0.01 | – |
| Bp4a | 243 | – | – | 0.03 |
| | 246 | 1.00 | 1.00 | 0.88 |
| | 249 | – | – | 0.09 |
| Bp5d | 215 | – | 0.01 | – |
| | 230 | 0.33 | 0.51 | 0.41 |
| | 245 | 0.03 | 0.06 | 0.08 |
| | 257 | – | 0.01 | – |
| | 260 | 0.63 | 0.38 | 0.52 |
| | 266 | – | 0.01 | – |
| Bp6b | 125 | 0.62 | 0.62 | 0.76 |
| | 131 | – | – | 0.24 |
| | 137 | 0.38 | 0.35 | – |
| | 155 | – | 0.03 | – |

of zooplankton in Québec lakes (Canada), and by Ng et al. (2009) in zooplankton community rock pools in Canada.

Our results of separating the variation of rotifer communities in anthropogenic water bodies show that the distance between water bodies may significantly affect how much the

**Table 4** Genetic variation of 7 microsatellite loci in 3 populations of *B. plicatilis*

| Locus | Variability measure | Population | | |
|---|---|---|---|---|
| | | A2G | A7G | B10G |
| Bp1b | $A_N$ | 3 | 4 | 5 |
| Total number of alleles: 6 | $H_e$ | 0.540 | 0.578 | 0.605 |
| 230–260 bp | $H_o$ | 0.733 | 0.912 | 0.879 |
| | $F_{IS}$ | −0.358 | −0.577 | −0.453 |
| | H–W test | 0.0000*** | 0.0000*** | 0.0000*** |
| Bp2 | $A_N$ | 4 | 6 | 3 |
| Total number of alleles: 7 | $H_e$ | 0.616 | 0.680 | 0.515 |
| 127–163 bp | $H_o$ | 1.000 | 0.941 | 1.000 |
| | $F_{IS}$ | −0.624 | −0.385 | −0.943 |
| | H–W test | 0.0000*** | 0.0000*** | 0.0000*** |
| Bp3 | $A_N$ | 2 | 5 | 4 |
| Total number of alleles: 6 | $H_e$ | 0.500 | 0.745 | 0.621 |
| 150–168 bp | $H_o$ | 1.000 | 0.971 | 0.879 |
| | $F_{IS}$ | −1.000 | −0.302 | −0.415 |
| | H–W test | 0.0000*** | 0.0000*** | 0.0000*** |
| Bp3c | $A_N$ | 2 | 6 | 4 |
| Total number of alleles: 7 | $H_e$ | 0.064 | 0.548 | 0.663 |
| 235–277 bp | $H_o$ | 0.000 | 0.235 | 0.000 |
| | $F_{IS}$ | 1.000 | 0.571 | 1.000 |
| | H–W test | 0.0169* | 0.0000*** | 0.0000*** |
| Bp4a | $A_N$ | 1 | 1 | 3 |
| Total number of alleles: 3 | $H_e$ | 0.000 | 0.000 | 0.219 |
| 243–249 bp | $H_o$ | 0.000 | 0.000 | 0.000 |
| | $F_{IS}$ | – | – | 1.000 |
| | H–W test | – | – | 0.0000*** |
| Bp5d | $A_N$ | 3 | 6 | 3 |
| Total number of alleles: 6 | $H_e$ | 0.487 | 0.585 | 0.562 |
| 215–266 bp | $H_o$ | 0.667 | 0.824 | 0.849 |
| | $F_{IS}$ | −0.370 | −0.408 | −0.511 |
| | H–W test | 0.0072* | 0.0012** | 0.0000*** |
| Bp6b | $A_N$ | 2 | 3 | 2 |
| Total number of alleles: 4 | $H_e$ | 0.473 | 0.493 | 0.367 |
| 125–155 bp | $H_o$ | 0.767 | 0.706 | 0.000 |
| | $F_{IS}$ | −0.622 | −0.432 | 1.000 |
| | H–W test | 0.0011** | 0.0000*** | 0.0000*** |
| Overall mean | $A_N$ | 2.429 | 4.429 | 3.429 |
| | $H_e$ | 0.383 | 0.518 | 0.507 |
| | $H_o$ | 0.595 | 0.655 | 0.515 |
| | $F_{IS}$ | −0.555 | −0.264 | −0.016 |

$A_N$ number of alleles, $H_e$ expected heterozygosity, $H_o$ observed heterozygosity, $F_{IS}$ inbreeding coefficient, *H–W test* probability of deviations from Hardy–Weinberg's equilibrium and their statistical significance determined by using Bonferroni sequential correction (Rice 1989; $k = 5$. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

**Table 5** Genetic variation between the studied populations of *B. plicatilis* ($F_{ST}$ values)

| Population | A2G | A7G | B10G |
|---|---|---|---|
| A2G | | 0.0529* | 0.1016* |
| A7G | 0.0529* | | 0.0517* |
| B10G | 0.1016* | 0.0517* | |

Statistically significant $F_{st}$ values after Bonferroni sequential correction (Rice 1989; $k = 3$; * $P < 0.05$)

local composition of rotifer communities is conditioned by dispersal. However, irrespective of distances between highly heterogeneous anthropogenic water bodies, local environmental conditions also strongly affect the species composition of rotifer communities. It seems that local environmental conditions are of major importance in shaping the rotifer communities in anthropogenic water bodies, while distances between the water bodies determine the possibilities of dispersal. That is why in group A significant and high values were recorded for spatial variables.

Ng et al. (2009) suggest that the confirmed significance of spatial variables jointly with environmental variables may reflect either a higher dispersal than in the perfect SS model, or a lower dispersal than in the perfect SS model. Division of the studied metacommunity into smaller groups and their analysis at 2 different spatial scales may help determine the true level of dispersal. This results from the fact that at a larger scale, dispersal cannot be higher than at a smaller scale. If the typical SS model was identified in a given metacommunity at a larger scale, then dispersal at a smaller scale may be either the same as in the perfect SS model or higher. The statistical significance of both environmental and spatial variables in group A indicates that dispersal is higher than in the perfect SS model.

Because of the smaller distance between local patches, dispersal may affect the rotifer communities more strongly, and the source-sink effect may determine to a large extent the local species diversity. Ng et al. (2009) suggest that if distances between local populations exceed 2 km, then dispersal is limited, while distances of less than 400 m allow a moderate level of dispersal. In our study, distances of about 1–3 km, enabled a moderate level of dispersal, while distances of 50–400 m allowed a higher level of dispersal which was probably made possible because the zooplankton could be transported by wind, water movements, waterfowl, amphibians, or humans.

It is necessary, however, to bear in mind that the studies of Ng et al. (2009) referred to crustaceans, not rotifers. As Cáceres and Soluk (2002) indicate, the dispersal of crustaceans is less effective. In addition the character of the water bodies which are being compared is different, and this might have had an influence on the results obtained.

A necessary condition for the shaping of community structure by environmental processes is that dispersal is sufficiently high to supply species to the sites that are suitable for them (Shurin 2000; Leibold and Norberg 2004; Cottenie 2005). Moderate dispersal allows changes in the local rotifer species diversity in cases of changes in local environmental conditions. As suggested by Cottenie et al. (2003) and Leibold et al. (2004), apart from necessary dispersal, species from other local habitats seem to affect the local communities only slightly. Many researchers believe that in most species of zooplankton, dispersal is limited and the local environmental conditions exert a major influence on the abundance and species diversity of local zooplankton communities (Shurin 2000; Shurin et al. 2000; Cottenie and De Meester 2003). Because of the limited, passive dispersal of freshwater plankton, species composition reflects habitat heterogeneity, and as a result, a high degree of correspondence is observed between the local species composition and local abiotic factors (Cottenie et al. 2003; Leibold et al. 2004; Cottenie 2005). In considerations concerning the effect of dispersal on local communities, its type may be important (Cottenie 2005). Research on zooplankton dispersal in habitat patches, such as lakes, ponds, reservoirs, or rock pools, indicate that zooplankton may be passively dispersed by birds (Figuerola and Green 2002) or wind (Cáceres and Soluk 2002). However, studies conducted by Jenkins and Underwood (1998) confirm that zooplankton is not dispersed as quickly as it is commonly assumed, and the rate of dispersal depends on environmental conditions. Those authors suggest that the probability of dispersal increases with age and degree of connection between the local habitats. All the anthropogenic water bodies analysed in our study were relatively young (most of them were created in the 1970s, and the 2 flood ponds in 1997), and they are not connected with one another, so dispersal should be rather limited. Probably thus it seems that the distance between the local water bodies has a stronger effect on the rate of dispersal than their age and degree of connection.

It is also noteworthy that the studied anthropogenic water bodies in the Silesian Upland are highly dynamic and variable. As suggested by Forrest and Arnott (2006), in ecosystems that are subject to frequent fluctuations of environmental conditions, dispersal plays a more important role than in stable ecosystems, and species are dispersed more quickly. Higher dispersal and the source-sink effect or the rescue effect (Gotelli 1991) in such variable habitats may be necessary to preserve local species diversity. Simultaneously, this is associated with an increase in species adaptability to the changing environmental conditions in dynamic habitats than in more stable habitats, e.g. in lakes (Leibold and Norberg 2004).

Dispersal plays an important ecological and evolutionary role (Dieckmann et al. 1999; Michels et al. 2001a). It affects not only the dynamics and persistence of local populations,

the rate of species extinction, and colonization of free patches, but also the species composition of the community (Jenkins 1995; Michels et al. 2001b) and the genetic structure of populations (McCauley 1991; Olivieri et al. 1995). Dispersal can be a significant indicator of local diversity and species composition through immigration from more variable habitats (Forrest and Arnott 2006). Migrants link populations genetically, and allow the colonization of free patches, preventing local extinction (Altermatt and Ebert 2008) through the rescue effect (Gotelli 1991). A high level of dispersal promotes gene flow and homogeneity between populations, whereas limited dispersal leads to divergence of populations due to genetic drift (including the founder effect) and natural selection (Slatkin 1985; Boileau and Hebert 1991; Jenkins and Underwood 1998; Michels et al. 2001a; Havel and Shurin 2004).

Analysis of microsatellite DNA polymorphism of *B. plicatilis* in 3 selected water bodies more or less distant from one another (about 1.0–3.5 km) provided valuable data on effects of dispersal and environmental conditions on local rotifer communities. The results show a high genetic variation within local populations, but the variation between populations was low. This indicates that gene flow occurs irrespective of the distance. Contrasting results were reported by Gómez et al. (2002a), who studied Spanish saline lakes, ponds, and lagoons. Those authors detected a very high genetic variation between the studied populations and a low variation within populations. However, it is necessary to stress that Gómez et al. (2002a) conducted their studies in water bodies which were more than a few kilometres distant from each other.

De Meester (1996) reviewed the available literature and found that zooplankton often shows a high genetic variation between populations, resulting from a limited gene flow because of local interactions, particularly competition with better genotypes of local inhabitants. Zooplankton organisms may be good colonists but other factors (e.g. local environmental conditions) lower the effectiveness of gene flow (De Meester et al. 2002; Gómez et al. 2002a; Campillo et al. 2009; Gómez 2005). This leads to a high genetic variation of the population at a regional scale.

Earlier research (Gómez and Carvalho 2000; Gómez et al. 2002a) showed that populations of *B. plicatilis* are in Hardy–Weinberg equilibrium. The cited authors recorded only a slight excess of homozygotes. In contrast, populations in our study were characterized by strong deviations from the equilibrium and an excess of heterozygotes. Their excess may result from selection for heterozygotes or the bottleneck effect. This effect is observed after a disaster (disease, drought, flood), when population size declines dramatically and its gene pool is reduced. This leads to a decrease in genetic diversity and changes in allele frequencies, whereas when the population size is increased, its genetic diversity is also greater. This is reflected in increased heterozygosity because of new mutations (Nei et al. 1975). It is possible that the *B. plicatilis* individuals collected for the present study originated from populations whose size is increasing after a decline due to the flood in 2010. It resulted in changes in environmental conditions, e.g. a decrease in concentrations of salts in the studied water bodies, and a decline of populations of *B. plicatilis*, followed by their gradual restoration. Probably, the observed low genetic variation between local populations could also be influenced by changes (homogenization) of environmental conditions after the flood.

A study of dormant eggs of these populations would probably explain the presence of a large quantity of heterozygotes. Hairston (1996) believes that the long-lived diapausing eggs of zooplankton constitute an ecological and evolutionary reservoir that can have an impact on the rate and direction of population, community, and ecosystem response to environmental change. But Brendonck and De Meester (2003) stated that "it is unknown and very difficult to measure what the effects of dispersal are on the dynamics of local egg banks. Depending on the type of habitat, resting stages can be dispersed to a variable degree by wind, water movements, waterfowl, amphibians, or humans".

To verify the results of this study, we found it necessary to repeat the analyses in a period when environmental conditions were more stable. However, irrespective of the causes of low interpopulation variation, results of this study indicate that rotifers can be dispersed over distances of more than 3.5 km.

This study will be followed by more detailed analyses, which should make it possible to assess precisely how much the environmental and spatial variables determine the local species diversity in dynamic, heterogeneous anthropogenic water bodies in the Silesian Upland. So far, over 2,400 water bodies have been created in this region due to casual or deliberate human activity (Rzętała 2008).

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